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RAY TRACHEIDS IN THE CONIFERALES[1]

RUTH HOLDEN

(WITH PLATES I AND II)

In classifying the various families of conifers from an anatomical standpoint, the structure of the medullary rays, whether fusiform or linear, thin or thick-walled, pitted or unpitted, has been a valuable criterion. Another feature which has not been emphasized as much as it deserves is the presence or absence of ray tracheids. DEBARY, MAYR, PENHALLOW, and others have reported them in certain genera, but to reach any conclusion of phylogenetic importance it will be necessary to consider the conditions affecting their appearance in all the main groups of conifers, extinct as well as living.

Extinct conifers

Succiniferous *Pityoxyla* of the Lower Cretaceous as described by JEFFREY and CHRYSLER (1) lack ray tracheids of any sort. In another less ancient cretaceous *Pityoxylon*, described by BAILEY (2), however, ray tracheids are present, both marginal and interspersed. Likewise in amber containing *Pityoxyla* from the Baltic deposits of the Late Eocene or Early Oligocene (3), marginal tracheids are present in the mature wood, though not in the early annual rings. In other types of fossil wood, namely *Cupressinoxylon*, *Cedroxylon*, *Taxoxylon*, *Araucarioxylon*, etc., ray tracheids have not been described.

Living conifers

ABIETINEAE

JEFFREY (4) has divided the Abietineae into two groups: the Pineae (*Pinus*, *Picea*, *Larix*, and *Pseudotsuga*) and the Abieteae (*Abies*, *Cedrus*, *Tsuga*, and *Pseudolarix*). Ray tracheids are present normally in all four genera of the Pineae, attaining their greatest complication in the hard pines, where they are dentate and reticulate. Of the Abieteae, ray tracheids are present normally in *Cedrus* and *Tsuga*. DeBary (5) and Penhallow (6) have both described them as characteristic of *Abies balsamea*, to which DeBary adds *A. excelsa*, but as lacking in other species of *Abies*. More recently Thompson has investigated this genus (7) and found them absent invariably in normal wood, but recalled in a number of species as a result of injury. Curiously, he reports them lacking in *A. balsamea*, an observation which I have confirmed from a study of seedling, mature wood, vigorous branches, roots, cone axes, etc., wounded and unwounded. In *Pseudolarix*, also, I have been unable to find ray tracheids, even in severely wounded branches. *Pseudolarix*, however, seems to be a particularly unfavorable subject for the study of experimental morphology, traumatic resin canals being formed much less readily here than in the other members of the Abietineae. The only remaining genus, *Keteleeria*, has the wood structure of *Abies*. Ray tracheids are entirely absent even in such primitive regions as the first annual ring, cone-bearing branch, cone axis, and are not recalled after wounding, though there is an abundant formation of traumatic resin canals.

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[1] Contributions from the Phanerogamic Laboratories of Harvard University. No. 48.

TAXODINEAE

The Taxodineae as a whole are simpler in wood structure than the Abietineae. The resin canals of the latter have disappeared here, except in *Sequoia* (8), their place being taken by resin cells. It would be natural to expect that the medullary rays also would be simpler, and this is indeed the case. The characteristically thick-walled, heavily pitted, parenchymatous ray cells of the Abietineae are replaced by thin-walled, sparingly pitted cells, and the ray tracheids characteristic of the Abietineae are lacking except under certain conditions to be described below.

The genus *Sequoia* undoubtedly stands nearest the Abietineae, since both living species have traumatic resin canals, and one fossil species (9), *S. Penhallowii*, has abundant pitting on the tangential walls of the ray cells, and crystals in the marginal cells like those of some species of *Abies*. Accordingly here if anywhere ray tracheids ought to be present, and Gothan has described them as of sporadic occurrence in the old wood of *S. gigantea* (10).

Fig. 1 represents a radial section of the wood of *S. gigantea;* fig. 2 a few cells of this ray at a greater magnification. Mixed with the typical parenchymatous ray cells, there are large square cells whose bordered pits on radial, tangential, and vertical walls prove them to be tracheids. This ray is unique, all others being composed of normal, horizontally elongated, parenchyma cells as shown in other parts of fig 1; and it is significant to note that the branch from which this section was cut had been badly wounded. This ray, however, occurred on the side of the branch opposite the wound, while the rays in the wound cap itself were perfectly normal. On examining other wounded specimens of *S. gigantea*, ray tracheids were found occasionally, always however in close proximity to the traumatic resin canals. All these other ray tracheids, moreover, were long and low, with bordered pits only on the horizontal wall next the parenchymatous ray cells.

Fig. 3 represents a ray from *S. sempervirens;* fig. 4 the same ray under a greater magnification. The ray tracheid here shown is like those commonly seen in *S. gigantea*, horizontally elongated, with bordered pits exclusively on the horizontal wall. Miss GORDON (**11**) has described ray tracheids in *S. sempervirens* and I have found them in every wounded piece examined, but not elsewhere. JEFFREY concluded from a study of resin canals that *S. gigantea* was more primitive than *S. sempervirens*, and the larger and more vigorous ray tracheids of the former corroborate his conclusion.

DEBARY has reported (**5**) ray tracheids in the monotypic genus *Sciadopitys*. My material consisted of a repeatedly wounded branch and possessed scattered ray tracheids of the type shown in fig. 5. Those described by DEBARY, however, were like those in hard pines, with "irregularly thickened ridges, projecting inward like teeth, on the upper and lower sides." The toothed cells I have seen were very rarely ray tracheids, but were rather of the nature of septate tracheids. Fig. 6 shows one of them.

Traumatic ray tracheids have been described by JEFFREY in *Cunninghamia sinensis* (**12**). It is interesting to note that he found them on the side of the branch opposite the wound, a condition like that mentioned above in *Sequoia gigantea*.

Specimens of *Taxodium distichum*, wounded and normal, of *Cryptomeria japonica*, and *Arthrotaxis selaginoides* were examined, but in none were ray tracheids observed.

CUPRESSINEAE

Of the genus *Chamaecyparis*, PENHALLOW (**6**) has described ray tracheids in *C. nootkatensis*, and absent elsewhere. In this species they are quite common, usually constituting the entire ray when one or two cells high, continuing for a time as such, and then becoming transformed into a parenchymatous ray. Careful examination, however, has revealed them in a number of other species. In *C. Lawsoniana* they are quite rare, but unquestionable. Fig. 7 shows their characteristic shape, long and low, with very small bordered pits next the parenchyma cells, two such pits being shown in the figure. *C. thyoides* and *C. plumosa* both show after injury tracheids of the same general appearance as those of *C. Lawsoniana*. A number of specimens of *C. pisifera* were examined before any ray tracheids were found. In one badly injured branch, however, there was a marked reversion to the thick-walled type of ray cell characteristic of the Abietineae, and between rows of these cells was a row of squarish tracheidal ray cells. In *C. obtusa* they seem entirely absent, even after injury.

In the closely allied genus *Cupressus* ray tracheids are much more common. Out of 7 species examined, they were present in 5; while of the other 2 species, only a small amount of material was available for study. The most frequent mode of occurrence is as an entire ray one to three cells high, though they have often been observed on the margin of higher rays. In this genus the relation to wounding is often diagrammatic. *C. guadalupensis*, after wounding, showed large numbers of ray tracheids. Fig. 8 shows a characteristic ray, but more commonly they constitute a ray one cell high, which soon turns into parenchyma; rarely they are marginal. *C. Macnabiana* presents the clearest case of traumatic reaction. Here frequently numbers of tracheidal rays one cell high start out immediately after a wound callus, extend through one or two years' growth, and then either die out or become transformed into parenchyma. *C. goveniana* showed the same thing, but to a less marked extent. *C. macrocarpa* was less favorable, but in one slightly wounded branch a few ray tracheids were observed. In *C. Benthami* they are very rare, but the material examined consisted only of a seedling with no wounds. Similarly a seedling of *C. tortulosa* failed to show any, and in *C. occidentalis* they seem to be entirely absent.

The southern hemisphere genus *Callitris*, with its sub-genus *Tetraclinus*, has been described by BAKER (**13**) as entirely without ray tracheids. JEFFREY, however, observed them in *Callitris* in connection with the leaf trace, and I have seen them quite widely distributed, but always in small numbers. Throughout the genus they are invariably marginal, never standing alone. Fig. 9 represents a characteristic ray tracheid in *C. arborea*. Two lots of material of this species were examined, and the mature wood of both contained ray tracheids of this type. There seemed to be no relation to injury, for they were equally abundant inside and outside a wound callus. Small branches, however, in neither lot showed ray tracheids. Fig. 10 demonstrates the type of tracheid characteristic of *C. calcarata*. Here they are longer and lower than in the above mentioned species, and, as there, the bordered pits are confined to the horizontal wall next the parenchyma cells. This material was entirely unwounded as far as could be seen. *C. columellaris* showed the same type of ray tracheids, even in normal tissue. *C. robusta* showed the largest number of tracheids of any species examined. They were present quite frequently in the mature wood, whether injured or not, but seem to be quite absent in the seedling stem. The ray tracheids are characteristically long and low, like those of *C. arborea*. *C. cupressoides*, as far as could be seen, lacks ray tracheids entirely, even in root wood. Fig. 11 shows a marginal tracheid in *Tetraclinus articulata*. They are present fairly abundantly in the mature wood, but are in general lacking in branches and twigs. One branch in which they were normally missing contained a few in the wound cap over a slight injury.

MAYR (**14**) has described ray tracheids in *Thuja plicata*, and I have found them quite common in both that species and in *T.*

occidentalis. Figs. 12 and 13 show a characteristic region of *T. occidentalis.* The tracheids are invariably marginal, with small bordered pits communicating with the parenchymatous ray cells, and slightly larger ones on their slanting end walls. *T. globosa* and *T. orientalis*, as far as examined, are entirely without ray tracheids, while in *T. dolobrata* they are rare.

PENHALLOW (**6**) has described ray tracheids in *Juniperus nana*, but states that they are lacking elsewhere in this genus. Wounds, however, in almost every species examined, sufficed to recall them. In *Juniperus* they occur usually as large, very irregularly shaped cells, thickly pitted on the tangential wall, constituting the whole of a ray one cell high. Rarely, also, they occur on the margin of parenchymatous rays, in which case the horizontal wall only is pitted. Fig. 14 shows a ray from *J. californica.* Ray tracheids have been observed in the following species: *J. californica*, *J. virginiana*, *J. pachyploea*, *J. scopulorum*, *J. occidentalis*, *J. chinensis*, *J. chinensis* var. *alba*, *J. sabina*, and *J. barbadensis.* In *J. communis* they were missing altogether from wounded seedling, stem, and root, except in the wound cap of one stem which had been repeatedly injured near the ground. Three species failed to show any: *J. bermudiana*, *J. californica* var. *utahensis*, and *J. macrocarpa.*

The genus *Libocedrus*, according to PENHALLOW, lacks ray tracheids. Figs. 15 and 16, however, show a ray of *Libocedrus decurrens* with a marginal tracheid. Toward the left of fig. 15 there is a bordered pit; fig. 16 shows it in greater magnification. This section was cut from wounded material, but other wounds examined failed to recall ray tracheids. Traumatic wood of *L. chilensis* and *L. doneana* seemed to be without them also.

Actinostrobus and *Fitzroya* (*F. Archeri* and *F. patagonica*) both lack ray tracheids, as far as investigated.

PODOCARPINEAE, TAXINEAE, AND ARAUCARINEAE

Saxegothaea, *Dacrydium*, *Podocarpus*, *Phyllocladus*, *Taxus*, *Torreya*, *Cephalotaxus*, *Araucaria*, and *Agathis* were examined, but no ray tracheids were observed.

Conclusions

To sum up, ray tracheids are present in *Pityoxyla* above the Middle Cretaceous; in all other fossil conifers they are absent. In living forms they occur normally in the Abietineae, traumatically in the Taxodineae and Cupressineae, but are invariably lacking in the Podocarpineae, Taxineae, and Araucarineae. Unless we are to assume that ray tracheids have developed independently in these groups, it is evident that the Taxodineae and Cupressineae must be related to the Abietineae. PENHALLOW admitted the relationship, but considered the cupressoid conifers ancestral to the Abietineae. The principle that traumatic tissue reverts to an ancestral type appears to be too strongly established to need discussion here. Applying this principle to the case in point, it must be seen that PENHALLOW has read the series in the wrong direction, and that the Taxodineae and Cupressineae are descended from rather than ancestral to the Abietineae. This conclusion might be questioned on the score that normally primitive regions, as first annual ring of seedling, root, cone axis, etc., fail to support the wound evidence by possessing ray tracheids. The answer to that appears to be simple: even *Pinus*, in which ray tracheids culminate, does not usually have them next the pith or in the cone axis. In other words, ray tracheids never made their way into the cone axis or first annual ring of any of the Abietineae, Taxodineae, or Cupressineae, but were characteristic only of mature wood. Consequently, now that they have become reduced in the last two families, they can be recalled only to the regions they once occupied normally. This conclusion as to the relative antiquity of the three groups, based on the distribution of ray tracheids alone, is corroborated by the conclusion reached by JEFFREY (4 and 8) from a study of resin canals.

The history of the development of ray tracheids, then, would be somewhat as follows. Up to the Middle Cretaceous, all *Pityoxyla* had simple medullary rays composed entirely of parenchyma. In the Middle Cretaceous they acquired ray tracheids. Some time between then and the Tertiary, a family sprung from these *Pityoxyla* characterized by the possession of ray tracheids. This family is the immediate ancestor of the Taxodineae and Cupressineae, while the original *Pityoxylon* line has persisted to the present day as the Abietineae. In some of them ray tracheids have become more and more elaborated (hard pines); in others they have become reduced until they occur only traumautically (*Abies*) or are entirely lacking (*Pseudolarix*). In the Taxodineae and Cupressineae they have become more and more reduced until they are present normally in only a very few species, and traumatically in certain others.

Since the taxads, podocarps, and araucarians never have ray tracheids, it is evident that if they came off from the Abietineae, it must have been at some time before the Middle Cretaceous, probably in the early Mesozoic.

To this suggested Upper Cretaceous origin of the Taxodineae and Cupressineae, it might be objected that in the Lower Cretaceous and Jurassic there are present *Cupressinoxyla*, together with leafy twigs, cone scales, cones, etc., which have been referred to *Sequoia* and allied forms. There is however nothing to prove that these woods belong to the Taxodineae or Cupressineae rather than to the podocarps or taxads, which, as pointed out above, probably originated very early in the Mesozoic. As to the twigs, cones, etc., wherever it has been possible to investigate their anatomy, they have been shown to be araucarians and not *Sequoia* at all (**15** and **16**).

Summary

1. Ray tracheids are present normally in *Pityoxyla* from the Middle Cretaceous on, and in the Abietineae.

2. Ray tracheids are present traumatically in the Taxodineae and the Cupressineae.

3. On the evidence of traumatic recapitulation of ancestral characteristics, it is evident that the Taxodineae and Cupressineae are descended from the Abietineae, having sprung from that line at some time after the Middle Cretaceous.

4. Since ray tracheids are universally absent in the Podocarpineae, Taxineae, and Araucarineae, these lines must have come off from the Abietineae at some time before the Middle Cretaceous.

5. These conclusions are corroborated by a study of geological records and of other anatomical structures, as resin canals, wood parenchyma, etc.

I wish to express to Dr. E. C. JEFFREY my thanks for material and for advice throughout the course of this investigation, and to Mr. W. P. THOMPSON, Mr. A. J. EAMES, and Mr. E. W. SINNOTT for material.

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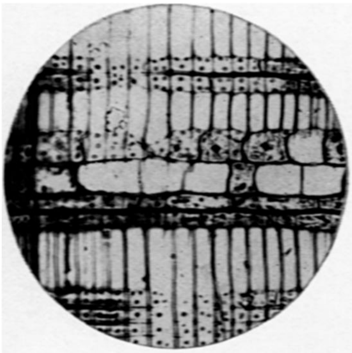
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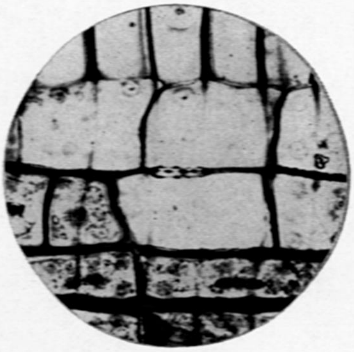
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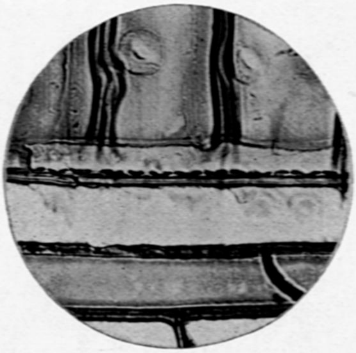
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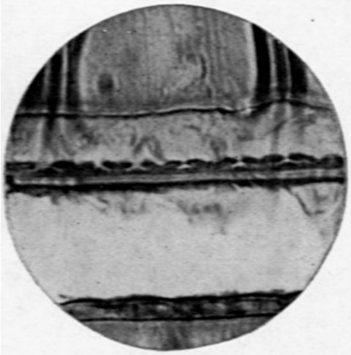
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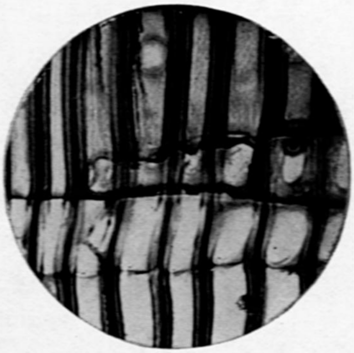
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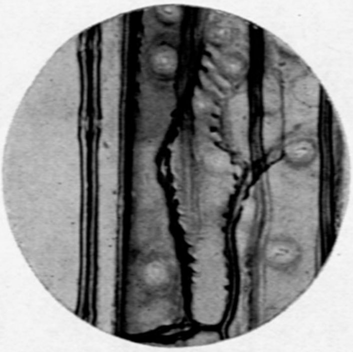
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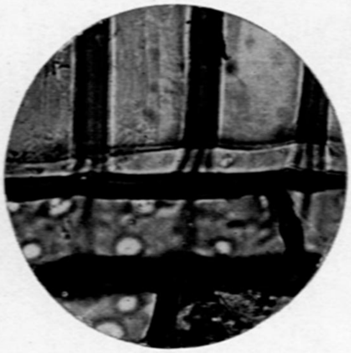
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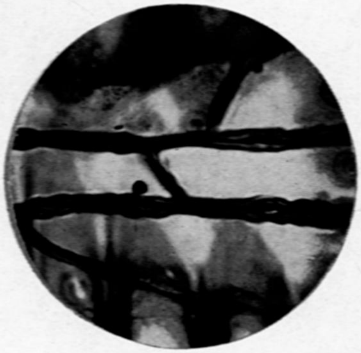
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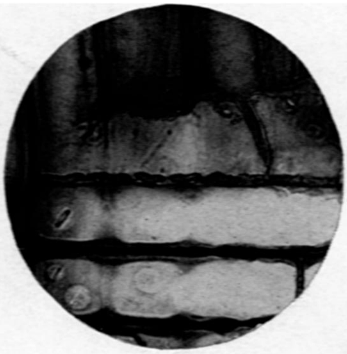
HOLDEN on RAY TRACHEIDS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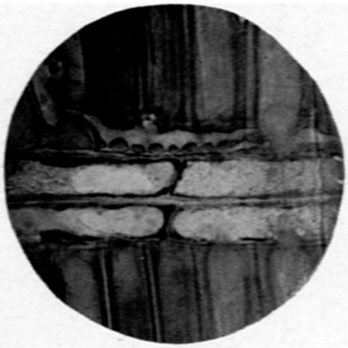
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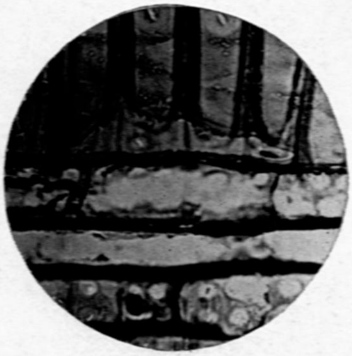
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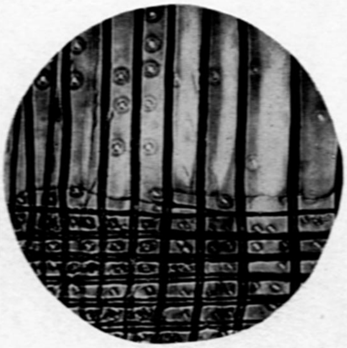
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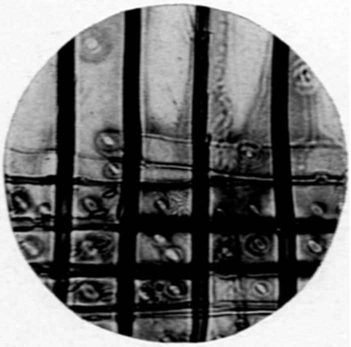
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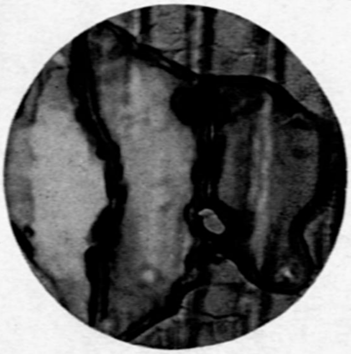
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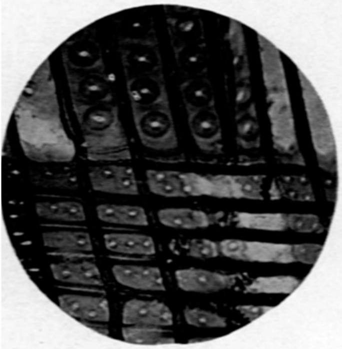
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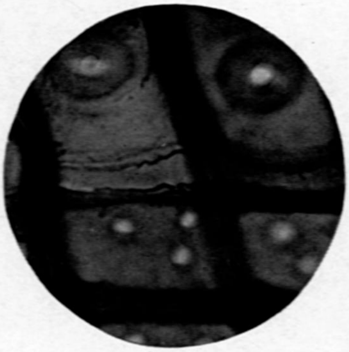
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HOLDEN on RAY TRACHEIDS

EXPLANATION OF PLATES I AND II

FIG. 1.—*Sequoia gigantea;* ×250.
FIG. 2.—Same; ×500.
FIG. 3.—*Sequoia sempervirens;* ×200.
FIG. 4.—Same; ×600.
FIG. 5.—*Sciadopitys;* ×400.
FIG. 6.—Same; ×600.
FIG. 7.—*Chamaecyparis Lawsoniana;* ×700.
FIG. 8.—*Cupressus guadalupensis;* ×600.
FIG. 9.—*Callitris arborea;* ×600.
FIG. 10.—*Callitris calcarata;* ×600.
FIG. 11.—*Tetraclinus articulata;* ×600.
FIG. 12.—*Thuja occidentalis;* ×200.
FIG. 13.—Same; ×700.
FIG. 14.—*Juniperus californica;* ×600.
FIG. 15.—*Libocedrus decurrens;* ×200.
FIG. 16.—Same; ×700.